THE FIRST TRUE ANOMIID BIVALVE?

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ABSTRACT. A new anomiid, here designated *Eonomia timida* gen. et sp. nov., is described from the Upper Bathonian and Oxfordian (Middle and Upper Jurassic) of England and Normandy. Its attachment to the substrate by pallial secretion, and the detailed structure of its ligamental area, distinguish it from later members of the family. Uncertainty about the taxonomic position of previously described pre-Cretaceous members of the family makes it a likely candidate for the earliest known anomiid.

THE Middle and Upper Jurassic rocks of southern England and Normandy constitute some of the best-known geological sections in the world. Their faunas have been studied and restudied by a succession of eminent palaeontologists and stratigraphers for more than 150 years; hence it was surprising to discover, at a number of different localities and stratigraphic horizons, common and well-preserved individuals of a distinctive species of bivalve mollusc which cannot be placed in any known Recent or fossil genus. The purpose of this paper is to describe the occurence, morphology, ecology, and evolutionary significance of these bivalves. All material is housed in the Oxford University Museum (Nos. OUM J 40184–40199 and OUM JZ 1782–1790).

OCCURRENCE

All known specimens of the bivalve here described consist of right valves firmly cemented to hard substrates. These substrates may be of organic origin (oyster shells, sponges, bone) or inorganic origin (hardgrounds). The specimens come from two broad stratigraphic intervals. The first is of Upper Bathonian age and corresponds to the zones of *Oppelia* (*Oxycerites*) *aspidoides* and *Clydoniceras discus*. In Normandy, specimens are common on the roofs of cavities beneath hardgrounds and on the sides of burrows which penetrate hardground surfaces. The hardground which incorporates the top surface of the lithistid sponge reefs at Luc-sur-Mer, Normandy (Fürsich and Palmer 1979) is a particularly good source of material. In England, the roofs of the cavities beneath the Bradford Clay hardground support many examples (Palmer and Fürsich 1974). They were misidentified as *Plicatula* sp. 2 in that account.

The second stratigraphic level which has yielded much material is the upper part of the Oxford Clay and the lower part of the Corallian (*mariae*, *cordatum*, and *plicatilis* Zones). In Normandy, exceptionally well-preserved material comes from the highest of these three zones, in the Argiles à *Lopha gregarea* near the top of the Falaises des Vaches Noires, east of Houlgate. In England, abundant material comes from the Upper Oxford Clay in the Oxford region, where they are found attached to oyster shells and plesiosaur bones. Considering how commonly valves of the new bivalve are found on these substrates in museum collections, it seems surprising that they have not been recognized and described before. Doubtless they occur elsewhere in England and northern France at localities where we have not searched for them.

MORPHOLOGY

The following description, unless otherwise stated, refers to the interior of the right valve (Pl. 99, figs. 1–6; text-fig. 1). Apart from a single specimen from the Oxfordian of Oxfordshire which shows a small fragment of the umbonal region of the left valve still emplaced above the corresponding position in the right valve (Pl. 99, fig. 6), all available material consists of right valves firmly cemented by pallial secretion to hard substrates.

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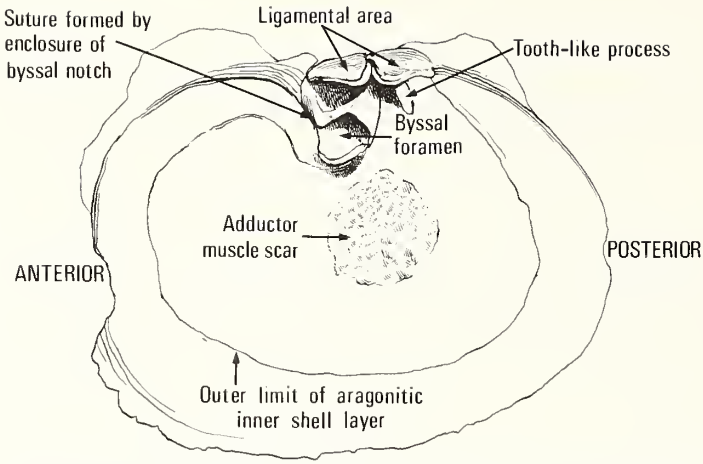

TEXT-FIG. 1. Line drawing of holotype of *Eonomia timida* gen. et sp. nov. (Pl. 99, fig. 1) showing hard-part morphology of the right valve.

The specimens are circular to subcircular (the length exceeding the height) in plan view, being flat or slightly bowl-shaped in accordance with the contours of the substrate to which they are cemented (Pl. 99, figs. 1, 5, 6). They range up to a height of 8 cm, but most specimens are in the order of 3–5 cm. The Oxfordian examples reach a larger size than those from the Bathonian, which do not exceed a height of 4 cm (Pl. 99, fig. 5). All specimens clearly show a central region formerly covered by a shell layer which has subsequently dissolved away to leave a shallow saucer-shaped depression (Pl. 99, fig. 1). This is inferred to have been the inner aragonitic shell layer, probably of cross-lamellar structure (text-fig. 1). This layer was covered on the outside by a well-developed and conspicuous layer of calcite folia which overlapped the presumed aragonite layer to form the inner face of the valve around the margin. The width of this lunate marginal region tapers to nothing in the dorsal shoulders of the shell, but ventrally reaches 2 cm in the largest examples. It is in turn covered on the outside by a thin (0·2 mm) layer of calcite prisms in some specimens. We have not been able to see this layer in all specimens. The thickness of the combined calcite layers in the ventral region where they account for the total valve thickness ranges from about 1 mm in the smaller specimens to just over 5 mm in a large specimen in which the shell had grown beyond the edge of the hard substrate. In this case, the outer surface of the free-growing part of the shell is seen to be thrown into irregularly concentric projecting rugae formed by the overlapping layers of calcite folia. The similarity of the shell structure of this part of the shell to that of oysters, together with the similar encrusting habit, is probably the main reason why these bivalves have previously been overlooked.

The specimens from the Oxfordian of Normandy are better preserved than any of the others, because traces remain of structures which are inferred originally to have been of aragonite (Pl. 99, figs 1–3). They are preserved

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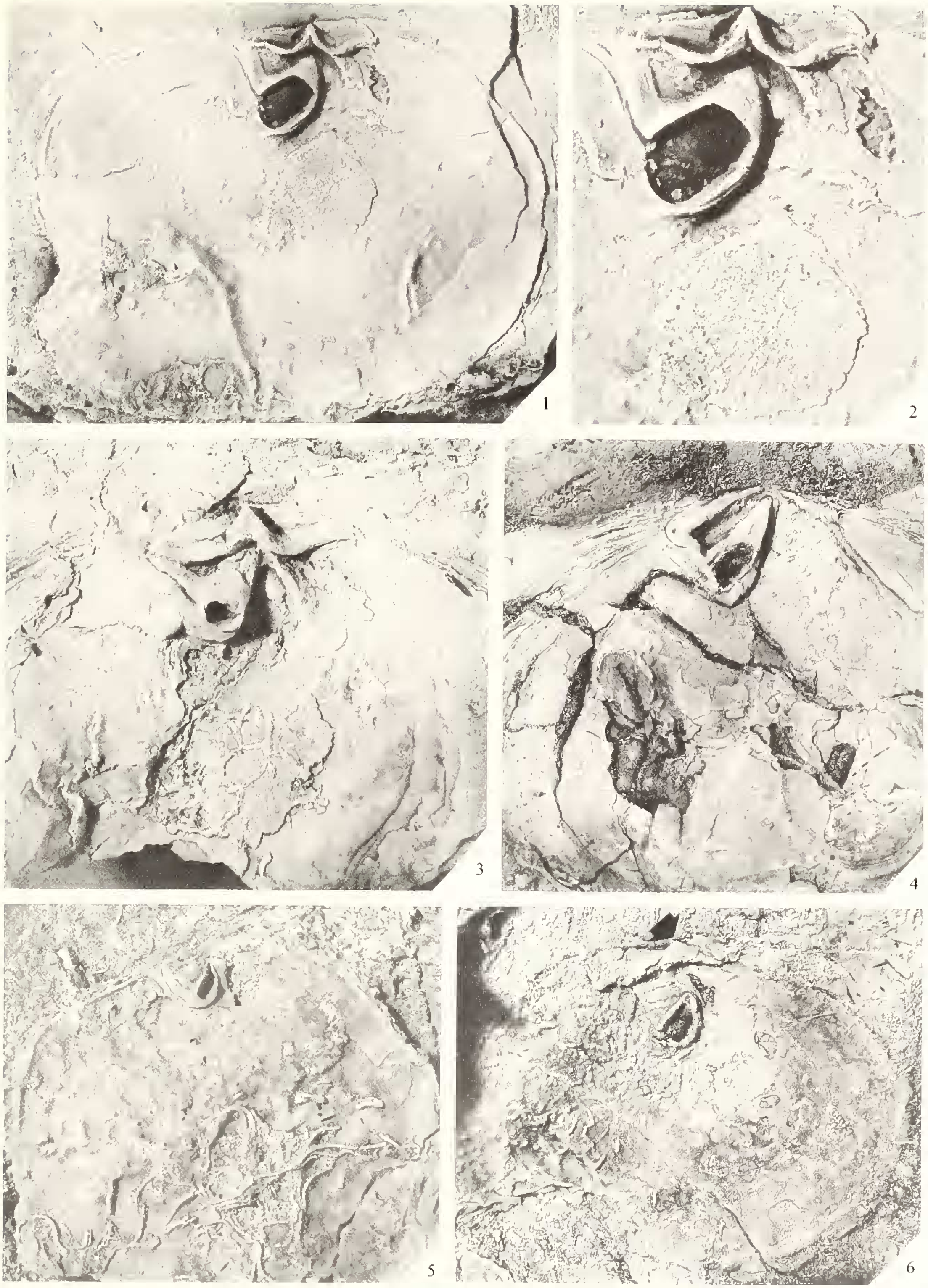
EXPLANATION OF PLATE 99

Figs. 1–6. Right valves of *Eonomia timida* gen. et sp. nov., attached to hard substrates by pallial secretion. 1, general view of holotype, OUM JZ 1782, from the Upper Oxfordian of Normandy, ×2·3. 2, close-up of specimen shown in fig. 1, showing ligamental area with tooth-like process emerging from its posteroventral margin, byssal foramen joined by a suture to the anterodorsal shell margin, and adductor muscle scar, ×4·5. 3, paratype from same locality as holotype showing the thickened and raised edge of the byssal foramen typical of adult specimens. OUM JZ 1783, ×2·2. 4, paratype from Upper Oxford Clay, Stanton Harcourt, Oxfordshire. Specimens from England show no trace of those features of the shell, such as the muscle scar and the ligamental area, which were originally composed of aragonite. OUM J 40195, ×1·8. 5, paratype attached to wall of burrow below hardground, Upper Bathonian, Ranville, Normandy. OUM JZ 1790, ×2·0 6, paratype from Upper Oxford Clay, Stanton Harcourt, Oxfordshire showing a fragment of the left valve still in position above the hinge of the right valve. Its umbo (arrowed) is marginal. OUM J 40199, ×2·2.



FÜRSICH and PALMER, anomiid bivalve

as a replacement in finely equigranular calcite (either a cement or a neomorphic replacement). The circular adductor muscle scar, presumably originally of myostracal prisms, is one such structure. It occupies a subcentral position such that its ventral margin roughly occupies the geometric centre of the shell. The other formerly aragonite structure seen only in the material from this one locality is the ligamental area, from the ventral margin of which a short tooth-like process extends in a posteroventral direction. The function of this process is not clear. The ligamental area is described further below.

The most conspicuous feature of the shell is a circular hole up to 3·5 mm in diameter in the largest specimens, which occupies a position just below the hinge line and just anterior of the dorsoventral axis (Pl. 99, figs. 1–6). Close study of the growth lines of the shell around this hole clearly shows that early in ontogeny it was an open notch beneath an anterior auricle, and that it must have remained open until the animal attained a diameter of about 1 cm. After this time it became occluded by adjoining of the outer shell layers of the anterior auricle and of the anterior shell margin, which swung dorsally around the hole to cut it off. The resulting join shows up as a short groove running from the anterodorsal margin of the hole to the front end of the ligamental area (Pl. 99, fig. 2; text-fig. 1). This hole was clearly occupied by a byssus in life, and its margins are made of the foliated calcite middle shell layer. In older specimens this margin thickens and becomes raised above the level of the inside of the shell (Pl. 99, fig. 3). The byssal threads laid down early in ontogeny appear to have remained attached throughout the subsequent growth of the shell, because the dorsal margin of the hole is seen to have lifted away from the substrate (over the dorsal byssal threads), as it grew in a ventral direction. The byssal hole thus looks today like a slipper with a dorsally directed pointed toe, the point of which lies just below the umbo.

The ligament appears to have been amphidetic but the ligamental area is divided into anterior and posterior portions which are mirror images about an axis which constitutes a perpendicular dropped from the umbo. The whole ligamental area thus has the form of a dorsoventrally flattened W (Pl. 99, figs. 1–3). The ventral edge forms an increasingly steep angle with the horizontal substrate during growth, so that in adult specimens, it and the edges of the central chevron of the W appear almost vertical (in a topographic sense) in the horizontal valve. It appears that in life the ligament must have passed over the dorsal edge of this chevron, hence introducing a dorsal element into the direction of the opening thrust. From the single poorly preserved fragment of left valve, attached to one of the specimens from the Oxfordshire Oxfordian (Pl. 99, fig. 6), it appears that the central chevron fitted into a corresponding triangular notch immediately below the left valve umbo. This umbo is clearly seen to be marginal.

TAXONOMIC AFFINITIES

The distinctive byssal foramen, which originates by complete enclosure of an anterior sub-auricular notch, is clearly reminiscent of the superfamily Anomiacea. An assignation to this group is further supported by the similarity of the shell structure to that of recent anomiaceans (Taylor, Kennedy and Hall 1969; Yonge 1977). The only other Jurassic genus known to have the byssal foramen is the pulvinitid *Hypotrema*, which is characterized by a multivincular ligament and an absence of foliated calcite from the shell.

The characteristics of the extant anomiaceans have recently been extensively discussed by Yonge (1977), who distinguishes two families—the Anomiidae and the Placunidae. Yonge further characterizes Recent anomiaceans by their monomyarian, pleurothetic (on the right valve) condition; their right twisted and hypertrophied byssal apparatus; their asymmetric ligament with projecting crurum on the right valve which introduces a dorsally directed element into the direction of the ligamental opening thrust; the supradorsal extension of the mantle lobes; and the calcified byssal secretion. Of these five characteristics, the first three are clearly exhibited by our animal, the fourth is hinted at, and the last was probably absent (not being necessary in a pallially cemented animal).

The form of the ligament in our animal differs from that in any of the Recent anomiaceans, being neither the boss on the end of a crurum typical of the anomiids, nor the inverted V-shaped structure found in the Placunidae. Nevertheless, we feel that both conditions could easily have arisen from our animal by modification of the central chevron in the W-shaped ligamental area. Swelling of this area in the ventral and dorsolateral directions would produce the sort of crurum seen in the anomiid *Pododesmus* (and incidentally in the typically anomiid Cretaceous genus *Paranomia*—see Wade 1926). On the other hand, reduction of the lateral parts of the ligamental area coupled with ventral growth of the descending arms of the central chevron produces the typically placunid structure. Indeed, a similar process is seen in the ontogenic development of *Placunanomia* (Yonge 1977).

The retention of the byssal foramen into adulthood and the inferred primitive phylogenetic position of our material justifies its being placed in the Anomiidae rather than the Placunidae, but the pallial cementation, the ligament characters, the probable lack of calcification in the byssus, and the marginal umbo justify creation of a new genus.

Superfamily ANOMIACEA Rafinesque, 1815
Family ANOMIIDAE Rafinesque, 1815
EONOMIA gen. nov.

Type species. Eonomia timida sp. nov.

Derivatio nominis. eos (Greek) = dawn.

Diagnosis. Pallially cemented anomiacean with distinct byssal foramen; ligamental area shaped like a flattened W with ventral margin raised; short tooth-like process extending below umbo in a posteroventral direction; umbo in left valve marginal; byssus probably uncalcified.

Eonomia timida sp. nov.

Plate 99, figs. 1–6; text-fig. 1

Holotype. From the Upper Oxfordian (*Plicatilis* Zone), Falaises des Vaches Noires, Normandy (JZ 1782).

Paratypes. JZ 1783–1786 from same locality as holotype; JZ 1787 from hardground immediately below sponge reefs at St-Aubin-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1788 from hardground at top of sponge reefs on foreshore at Luc-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1789 from fossiliferous clay beneath Calcaire de Langrune, Lion-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1790 from hardground at top of Calcaire de Ranville, Ranville Cement Works, Normandy (Upper Bathonian, *aspidoides* Zone); J 40190–40199 from Upper Oxford Clay, Stanton Harcourt, Oxfordshire; J 40187–40189 from Upper Oxford Clay, Cowley (*mariae* or *cordatum* Zone); J 40184–40186 from hardground at base of Bradford Clay, Bradford-on-Avon, Wilts. (Upper Bathonian, *hollandi* subzone).

Derivatio nominis. timidus (Lat.) = shy, retiring, wary of discovery.

Diagnosis. Circular or subcircular *Eonomia* up to at least 8 cm in height; ventral edge of byssal foramen never exceeds a quarter of the distance between the umbo and the ventral margin; well-developed aragonite inner shell layer overlapped by a wide expanse of the middle foliated calcite shell layer, which forms the inner surface of the valve anteriorly, posteriorly, and ventrally.

PALAEOECOLOGY

Eonomia timida occurs in two broad habitats: under recesses and in cavities beneath hardgrounds, and on biogenic hard substrates in muddy environments. Bathonian specimens are known only from the former habitat. They occur on the walls of lithified burrow systems, on the roofs of hardground cavities or recesses, and on the lower surfaces of *Platychonia*, a lithistid sponge forming small sponge reefs at St-Aubin and Luc-ser-Mer (Normandy) (Fürsich and Palmer 1979; Palmer and Fürsich 1981). In contrast, in the Lower to Middle Oxfordian, they are known encrusting *Liostrea*, *Gryphaea*, and the vertebrae or other bones of plesiosaurs. In this case they appear to have lived on upper surfaces. The occurrence at Vaches Noires is within the oyster/*Isognomon promytiloides* association (Fürsich 1977), which occupied a low-energy, offshore environment characterized by low sedimentation rates and a fine-grained substrate. The latter was probably somewhat firmer than that represented by the bulk of the Oxford Clay.

Three possible explanations are offered for the occurrence of *E. timida* in two distinct habitats:

(*a*) The distribution pattern is a result of collection failure rather than an original feature and thus of no significance. However, in the search for further specimens of *Eonomia*, a great variety of substrates and habitats within the Jurassic have been examined, and it appears that the known distribution pattern is a primary feature.

(*b*) A shift in habitat occurred during the course of the Jurassic from cavities to exposed hard substrates, possibly in conjunction with a better adaptation to cope with water rich in suspended sediment particles.

(*c*) Bathonian and Oxfordian forms represent two different species each restricted to a particular habitat.

Although there are certain morphological differences between the two groups of specimens (e.g. a larger size of the Oxfordian specimens), we feel that they do not merit specific separation. We therefore think that a shift in habitat is the most likely explanation for the observed distribution pattern of *Eonomia*. Recent Anomiacea are particularly well adapted to life on muddy substrates as their foot serves as a highly efficient organ for cleansing the mantle cavity (Yonge 1977). It is therefore suggested that, as Bathonian forms needed clear water (usually associated with hardgrounds) and could not cope with sediment influx (hence their preference for cavity roofs) and Oxfordian forms were well adapted to live in turbid environments, the change in habitat was due primarly to the increased efficiency of the foot in cleaning the mantle cavity. The problem as to why *Eonomia* has a centrally placed byssus lasting throughout life, as well as being cemented to the hard substrate (a marked case of belt and braces) is probably also solved by a consideration of cleansing habits. Recent anomiids have a very small proportion of catch to quick muscle in the adductor, whose function is largely given over to rapid contractions of the valves to eject faeces and pseudofaeces (Yonge 1977). It is the hypertrophied byssal retractor muscle that thus takes over the business of holding the valves closed for longer periods of time.

EVOLUTIONARY SIGNIFICANCE

The early evolutionary history of the Anomiacea is very confused, and the pre-Cretaceous ranks of the superfamily are largely composed of imposters and cripples. The only serious Palaeozoic contender for a place in the group is the Permian *Permanomia* (Newell and Boyd 1970). This genus, however, like previously proposed Palaeozoic contenders (see Stoliczka 1870–71) is too poorly known to be certain of inclusion. The critical right valve is unknown (probably it too was cemented), and the anomiid designation is made on the basis of the left valve musculature and a putative calcified byssus attached to the inside of the left valve in one specimen. The unlikely position of this latter feature surely makes it more likely to be an artefact, and the left valve musculature by itself is not enough (as Newell and Boyd (1970) point out) to ensure the certain familial affinity. Similar musculature would be expected, for example, in the early Pulvinitidae. *Permanomia* further has a duplivincular ligament, although this could give rise to the simpler alivincular ligament of true anomiaceans by neotenous retention of the primary ligament (Trueman, *in* Cox 1969). The verdict on *Permanomia* therefore must be 'not proven', but even if a right valve with the appropriate shell structure and an enclosed byssal notch were found tomorrow, the difference in the ligament should surely justify a separate family within the superfamily.

References to Jurassic *Anomia* are widespread in the literature (e.g. Buvignier 1852) and we have examined material from three museums with good collections of Jurassic bivalves where examples of such *Anomia* might be expected. These collections are those of the Oxford University Museum, the British Museum (Natural History), and the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Every single putative Jurassic *Anomia* in these collections is either totally unrecognizable, or else attributable to the genus *Placunopsis*. It is our opinion that confusion with this latter species is responsible for the vast majority, and perhaps all, of Jurassic *Anomia* records. The left valves of *Placunopsis* consisted of an inner aragonite layer and an outer foliated calcite layer which invariably became worn off in the umbonal region. Thus, when the aragonite layer was dissovled away during diagenesis, the remaining calcite layer appeared to be perforated by a hole in the umbonal region that has often been mistaken for the anomiid byssal foramen. *Eonomia timida* is therefore the earliest unequivocal anomiid known to us.

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